

THE PERMIAN LYCOPOD *CYCLODENDRON* *LESLII* FROM SOUTH AFRICA

by R. J. RAYNER

ABSTRACT. Well-preserved axes of the southern hemisphere Permian lycopod *Cyclodendron leslii* (Seward, 1903) are described from localities in South Africa. New information includes details of the cuticle with stomata, epidermal cells, leafy vegetative axes, and fertile axes. *C. leslii* was an arborescent heterosporous lycopod with a restricted stratigraphic range, and it formed a small but significant part of the *Glossopteris* flora of South Africa.

IMPRESSION fossils from Vereeniging, Atherstone Quarry, and Port Alfred, South Africa, were described by Seward (1903) under the name *Bothrodendron leslii*. He noted dichotomous branching of leafless axes and variation in size, frequency, and appearance of leaf scars; his choice of genus was influenced by a strong resemblance of the South African material to *B. kiltorkense* from Ireland. The Vereeniging material was later figured by Arber (1905) who formalized a diagnosis of *B. leslii*. The assignment of these axes to a northern hemisphere genus was not altogether popular, leading Kräusel (1928) to erect a new genus *Cyclodendron*, based upon well-preserved leafy material from the Ecca beds in South West Africa; he also included Ugandan material and the specimens previously described by Seward (1903). Du Toit (1932) accepted the validity of Kräusel's genus and gave a comprehensive account of the vegetative axes of Ugandan *Cyclodendron*. In discussing the geographical distribution of *C. leslii* (Vereeniging, Vierfontein, (?) Newcastle, Goamus, Wankie, east Tanganyika, Lukuga, and west Lake Tanganyika) in the Karoo beds of Africa, du Toit (1932) pointed out the limited stratigraphic range of the species. The monospecific genus seemed secure; it had a characteristic morphology and was considered to be geographically and stratigraphically restricted.

Edwards (1952), however, re-examined the southern hemisphere lycopods housed in the British Museum (Natural History) and followed White (1908) by placing them all in the Brazilian species *Lycopodiopsis pedroanum*, a species characterized by the absence of both a central leaf scar and parichnos scars. The Brazilian specimens of *L. pedroanum* have been recently redescribed as *Brasilodendron pedroanum* by Chaloner *et al.* (1979). The former name is now reserved for permineralized material showing internal anatomy, while the latter is used for material with preserved outer morphology.

The taxonomic arguments over the treatment of southern hemisphere Permian lycopods were partially resolved by Kräusel (1961) who illustrated and described a fertile *Cyclodendron* axis. Subsequent authors, however, have not been consistent in their identification of *C. leslii* from Africa (e.g. compare Plumstead 1961 and 1973); the genus requires thorough description, particularly of details of fertile organization. New collections from several localities within the Ecca sediments have revealed details of fertile axes, leaf morphology, and cuticle that show *Cyclodendron* to be a distinctive genus, differing significantly from other coeval southern and northern hemisphere lycopods.

MATERIALS AND METHODS

This paper is based on fossil plants found at two Permian localities, Vereeniging and Hammanskraal, South Africa. Three authors have worked on parts of the well-preserved Hammanskraal assemblage: Plumstead (1969) described two large fructifications; Kovács-Endrödy (1974, 1976) reported fertile and vegetative *Glossopteris* leaves; and Smithies (1978) reviewed the complete assemblage. Their material, and the specimens described in

this paper, were collected from a disused refractory brick quarry about 7 km south of Hammanskraal in the central part of Transvaal Province. The fossils are coalified compressions (*sensu* Schopf 1975), some with cuticle.

Large numbers of plant fossils from the Vereeniging locality are housed at the Bernard Price Institute, University of Witwatersrand, Johannesburg; attached glossopterid fructifications were discovered among them and described by Plumstead (1952), while I have found and described here a number of impressions of fertile *Cyclodendron* axes. The locality has been thoroughly described by le Roux and Anderson (1977). The *Cyclodendron* axes are preserved either as endocortical casts or impressions in a very fine-grained matrix. Chaloner *et al.* (1980) reviewed this form of preservation where, after burial and presumed partial decomposition of tissues, mud infilled a cortical cavity. Subsequent compression and collapse of the plant tissues produced a cast of the mud infill. Leaves are exclusively impressions while axes are both endocortical casts and impressions of casts in the matrix. The outer surface of the stem cast closely resembles the original plant surface because the matrix is so fine grained. Indeed, the outline of some epidermal cells is preserved, presumably as an impression of the inner surface of the cuticle on the mud infill prior to consolidation of the sediment. No organic matter remains but the specimens are invaluable in providing details of gross morphology of leaves, leaf scars, and fertile axes.

Macrospecimens, both impressions and compressions, were uncovered using steel needles ('dégagement' of Leclercq 1960). The specimens were repeatedly photographed during development. Impression fossils were photographed under unidirectional lighting. Portions of well-preserved impressions showing features of the epidermis were mounted on stubs for scanning electron microscopy. Cuticles were carefully removed from the Hammanskraal coalified compressions with a fine brush, oxidized with Schulze, neutralized in dilute alkali, washed, and mounted on glass slides or directly on to SEM stubs. Photomicrographs were taken on Wild M8 (incident light) and Zeiss (transmitted light) microscopes.

Smithies (1978) reviewed several of the Ecca plant-bearing localities and, on macroplant evidence, placed both Vereeniging and Hammanskraal in Plumstead's (1966) floristic zone III or basal IV with a lower Permian age. Anderson (1977) studied the palynology of Hammanskraal and placed the assemblage in the middle Ecca, also with a lower Permian age.

All specimens are housed in the Bernard Price Institute (BP).

SYSTEMATIC PALAEONTOLOGY

Division TRACHEOPHYTA

Class LYCOPSIDA

Order LEPIDODENDRALES

Family LYCOPODIOPSISACEAE

Genus CYCLODENDRON Kräusel, 1928

Type species. *C. leslii* (Seward, 1903).

Diagnosis. Arborescent lycopod; stems covered with oval leaf scars or laminar leaves borne in a low angle spiral; branching occasional and dichotomous; heterosporous with unisexual subterminal fertile zones.

EXPLANATION OF PLATE 11

Figs. 1-9. *Cyclodendron leslii* (Seward, 1903). 1, BP/2/13456, dichotomously branched axis with spirally arranged leaf scars; there is a small zone of larger scars towards the base of the axis, $\times 1$. 2, BP/2/13315, broad leafless striated axis, $\times 0.8$. 3, BP/2/1327a, details of leaf scar on a broad striated leafless axis; the oval scar is flanked by diamond-shaped impressions with a central longitudinal depression, $\times 9$. 4, BP/2/13456, leaf scars; arrow indicates small, presumably vascular pit on the umbo, $\times 7$. 5, BP/2/13256, terminal leafy axis, $\times 0.5$. 6, BP/2/13232, leafless curved axis with narrow central strand (arrowed), $\times 1.1$. 7, BP/2/13457, terminal axis; the large rounded apex is shrouded by a crown of microphylls, $\times 1$. 8, HKS/1, surface of compressed axis showing details of elongate to isodiametric epidermal cells; arrows indicate depressions surrounded by a group of six or seven epidermal cells, SEM micrograph, $\times 50$. 9, BP/2/13462, two groups of microphylls, probably borne on terminal axes, compressed into a fan-shaped pattern; median vascular strand of leaf arrowed, $\times 0.5$.



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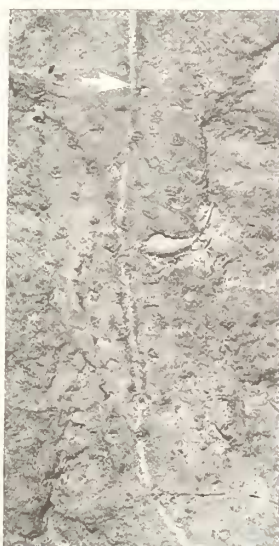
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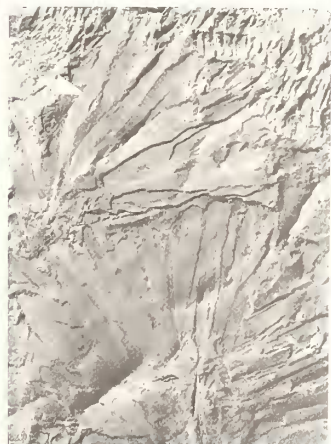
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Cyclodendron lesliei (Seward, 1903)

Plates 11–13; text-fig. 1

Synonymy. See Kräusel (1961).*Holotype.* South African Museum 13691 (Seward 1903, pl. 11, fig. 1).

Emended diagnosis. Axes 8 mm–8 cm wide, covered with leaves (axes < 2 cm) or leaf abscission scars (axes > 2 cm); microphylls 3–4 mm wide, up to 8 cm long, with pointed apex and single undivided vascular strand; sunken oval leaf scars containing an umbo just above the centre with small round vascular pit; epidermal cells slightly elongate to isodiametric, 33–120 μm long by 21–45 μm wide; stomata consisting of a central slit-like pore encircled by two narrow guard cells, with cuticle extending into the pore and around the guard cells; stomata (pore and guard cells) 30–60 μm long, 15–27 μm wide; heterosporous with unisexual subterminal fertile zones, microsporangia 3 mm in diameter; megasporangia 1 cm in diameter, containing a single tetrad of megaspores up to 6 mm in diameter; zones of microsporophylls and megasporophylls borne directly on the main axis.

Description. Axes are assigned to *C. lesliei* on the distinctive morphology of leaf scars, leaves (where present), and details of the epidermis (cuticle and epidermal cell impressions). There is a danger of misinterpreting surface topography of axes: casts faithfully represent the original surface features, whereas impressions show the reverse. Axes vary in width from 8 mm to over 8 cm. The most conspicuous features of vegetative axes are leaf abscission scars on all parts devoid of leaves (Pl. 11, figs. 1, 2). The scars are oval in outline, widely spaced, and arranged in a low angled spiral with ten to fourteen per gyre. Each scar consists of an oval depression with a raised portion (umbo) just above the centre (Pl. 11, fig. 4). The umbo on a few examples has a small round central pit (Pl. 11, fig. 4, arrowed), presumed to be the site of the vascular trace. There is no leaf cushion. Leaf scars on some wide axes are frequently flanked by indistinct, diamond-shaped areas (Pl. 11, fig. 3) which may be parichnos scars. The wider axes also commonly have a striated appearance (Pl. 11, figs. 2, 3) produced by small transverse ridges.

A narrow ribbon-like strand is preserved in several specimens. The strand is up to 2 mm wide and is either centrally placed or follows a sinuous path through the cortical region (Pl. 11, fig. 6, arrowed); I interpret the strand as xylem. Since several narrow axes are curved (Pl. 12, fig. 3; Pl. 13, fig. 5), it seems possible that they were pliable, rather than rigid, and more prone to twisting during post-mortem transport and burial. However, I consider *Cyclodendron* to have been arborescent and the tips of some terminal axes may have originally been recurved and pendulous, as in many arborescent lycopods.

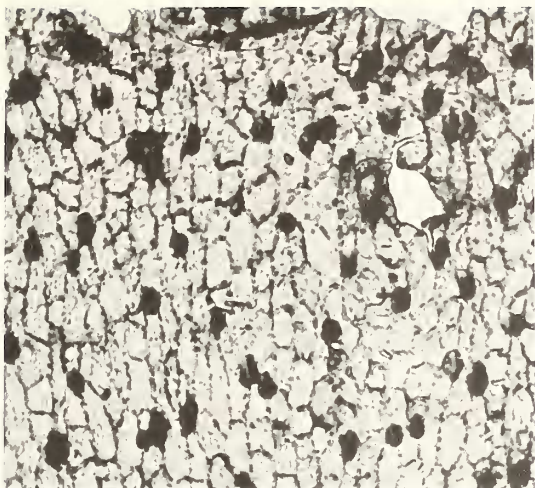
All axes wider than 2 cm are leafless, and their leaf scars are therefore evidence for abscission. Narrower specimens are commonly covered with leaves. One axis, just 2 cm wide, has a few leaves still attached (Pl. 12, fig. 3). One specimen shows details of a terminal axis (Pl. 11, fig. 7): the apex is rounded, just over 1 cm wide, and shrouded in leaves. Of the several hundred specimens examined, branching was only observed in three specimens; in each, divisions are dichotomous (Pl. 11, fig. 1). Branching axes are about 1.5 cm wide.

The leaves are laminate with approximately parallel edges that taper abruptly to a point at the apex (Pl. 13, fig. 2). They are up to 8 cm long and 3–4 mm wide, and so numerous on terminal axes that they are compressed

EXPLANATION OF PLATE 12

Figs. 1–7. *Cyclodendron lesliei* (Seward, 1903). 1, HK/34, cuticle with reticulum of epidermal cell impressions; black spots correspond to stomata, $\times 85$. 2, HKS/2, internal surface of cuticle showing cell flanges, $\times 80$. 3, BP/2/13455, bent, partially leafy axis showing variation in size of leaf scars; larger scars appear closer together (arrowed) and may correspond to attachment points of sporophylls, $\times 0.5$. 4, HKS/2, stoma showing upstanding flanges believed to be an extension of cuticle down into pore and over guard cells, $\times 1000$. 5, HK/34, indistinct epidermal cell flanges around stoma consisting of thickened cuticle with oval outline and central elongate pore (dark line), $\times 1000$. 6, HK/34, cuticle with rounded internal thickening showing annular gap and associated cracks, $\times 500$. 7, HK/34, internal cuticular thickening; margin extends between adjacent epidermal cells, $\times 600$.

1, 5–7, light micrographs; 2, 4, SEM micrographs.



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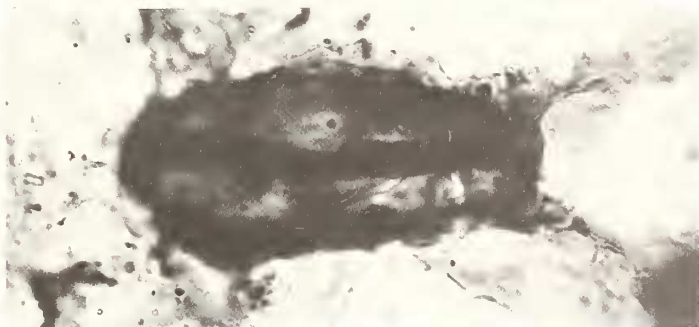
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into fan shapes (Pl. 11, figs. 5, 7, 9). Each leaf has a single, undivided, median vascular strand (Pl. 11, fig. 9, arrowed). The surface of the leaf impression is smooth, in contrast to the cellular topography of the axes.

So fine is the matrix at Vereening that outlines of individual epidermal cells have been preserved (Pl. 11, fig. 8), identical in shape and size to the cellular pattern preserved on the inner surface of cuticle from Hammanskraal (Pl. 12, fig. 2). The cells are slightly elongate to isodiametric; elongation is either parallel to the long axis of the stem, or in a radiating pattern around scars. Interrupting the general pattern are small groups of six or seven cells which surround a depression that is itself about the size of one cell (Pl. 11, fig. 8, arrowed). These depressions are probably stomata.

Cuticle was removed from coalified compressions in the areas between leaf scars, there being no evidence of cuticle over the scars themselves. The epidermal cell impressions are delimited by cuticular flanges shown as dark lines on light micrographs (Pl. 12, fig. 1), and upstanding ridges on scanning electron micrographs of the cuticle's inner surface (Pl. 12, fig. 2). The cells are 33–120 μm long and 21–45 μm wide ($\bar{x} = 68 \times 30 \mu\text{m}$, 180 measurements). In addition to the epidermal cell impressions there are numerous, small, circular to lens-shaped dark areas (Pl. 12, fig. 1) which correspond to thickenings on the inner surface of the cuticle (Pl. 12, fig. 4). The lens-shaped or oval thickenings often have a longitudinal slit-like pore in their centre (Pl. 12, fig. 5), resembling a stoma. Some of the circular thickenings, however, have an annular gap in the form of either a complete or incomplete ring (Pl. 12, fig. 6); occasional examples have a radiating pattern of cracks. I interpret this ring with associated cracks to be the result of damage during compression. Also, the circular thickening in a few examples extends between adjacent epidermal cells (Pl. 12, fig. 7). I regard the lens-shaped areas with pores as stomata and suggest that cuticle originally extended down into the pore and around the guard cells. The circular areas with no evidence of pores may possibly represent trichome bases, but no hairs were found attached; I think it unlikely that such internal thickenings would be associated with trichome bases, and more probable that they also represent stomata. Assuming all the dark areas to be stomata, the stomatal index varies between twelve and sixteen. The stomatal apparatus thus consists of a slit-like pore encircled by two elongate guard cells (Pl. 12, fig. 5) which are considerably narrower than the surrounding epidermal cells. The stomatal apparatus (pore and guard cells) is 30–60 μm long and 15–27 μm wide (ninety-nine measurements). Plate 12, fig. 4 shows an internal flange which I regard as cuticle extending down into the pore and which probably covered the underside of the guard cells. The inner thickening was formed by compression during fossilization (text-fig. 1D–F).

Several axes bearing both microsporangiata and megasporangiata zones have been found. The axes are all leafy and 1.0–1.5 cm wide (Pl. 13, fig. 1); I regard them as fertile from the evidence of impression fossils alone. The microsporangiata zones are subterminal in position and are identified by the modified sporophylls. These leaves differ from the others, being recurved close to the point of attachment, and they occur in discrete zones (Pl. 13, figs. 1, 4). Microsporangia are apparently borne singly and are small (up to 3 mm diameter) rounded bodies preserved mostly on the axes. A few examples occur in association with sporophylls (Pl. 13, fig. 4, arrowed). Each microsporangium was held in a cup-like structure formed by the curve in the sporophyll (text-fig. 1B, C). Repeated attempts to obtain *in situ* microspores failed and no dispersed spores were recovered from macerating fragments of the sediment. Evidently, all organic matter has been removed.

Megasporangia are preserved in clusters, on or close to axes (Pl. 13, fig. 3). Preservation is poor, yet Plate 13, fig. 3 shows five megasporangia, each on a sporophyll, close to the point of attachment. Each megasporangium is circular to subtriangular in outline, up to 1 cm in diameter, and appears to contain a single tetrad of large spores (Pl. 13, fig. 6). Each megaspore may be up to 6 mm in diameter. Plate 13, fig. 6 shows a triradiate megaspore (arrowed) in a group of three, presumably part of a tetrad. Plate 12, fig. 3 shows a zone of leaf scars of different sizes which may be related to the position of sporophylls. The presence of leaves on this possibly fertile axis suggests that sporangia may have been abscised with the sporophylls.

EXPLANATION OF PLATE 13

Figs. 1–6. *Cyclodendron lesliei* (Seward, 1903). 1, BP/2/13461, terminal leafy axis with microsporangiata zone in subterminal position (double arrow marks extent of fertile zone); sporophylls are curved close to their point of attachment, $\times 0.6$. 2, BP/2/13287, probable microsporangiata zone with well-preserved leaf impressions, $\times 0.8$. 3, BP/2/13257a, five megasporangia associated with sporophylls, $\times 0.9$. 4, BP/2/13460, leafy microsporangiata axis with straight microphylls above zone of recurved sporophylls; arrows indicate position of two microsporangia, $\times 0.5$. 5, BP/2/13454, bent, leafless branching axis with central vascular strand (arrowed); axis shows variation in frequency of scars, $\times 0.4$. 6, BP/2/13459, subrounded megasporangium showing three spores of presumed tetrad; arrow indicates triradiate mark, $\times 4$.



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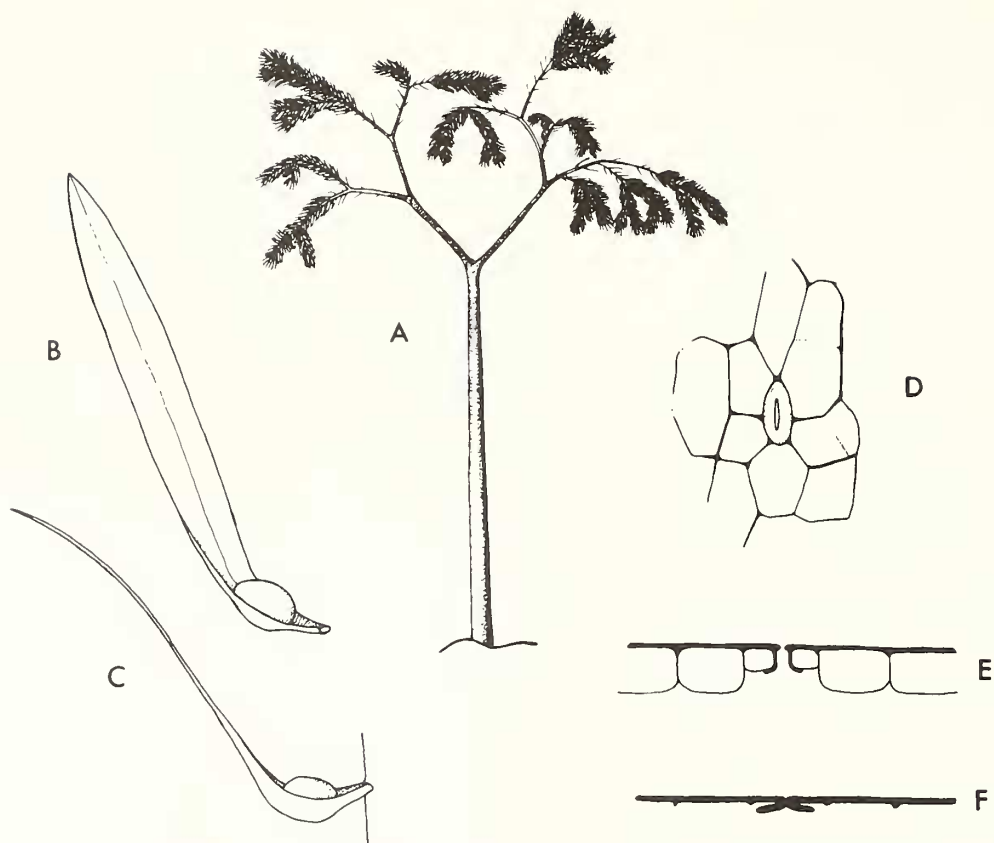
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TEXT-FIG. 1. Reconstructions of *Cyclodendron leslii* (Seward, 1903). A, speculative reconstruction showing arborescent growth habit, occasional dichotomous branching, and leafy terminal axes (some bearing subterminal fertile zones). B, oblique view and C, side view of microsporangiate sporophyll, actual size; the sporangium probably sat in a cup formed by a bend in the sporophyll. D, fossil stoma consisting of elongate pore encircled by thickened cuticle and surrounded by epidermal cell impressions, $\times 200$. E, transverse section of stoma showing original arrangement of cuticle extending down into pore around guard cells. F, cuticle in E after fossilization; cuticle that extended into pore has been compressed, forming two internal flanges (cf. Pl. 13, fig. 3).

Discussion. Three genera of southern hemisphere Permian lycopods have been reported: *Cyclodendron* Kräusel, 1928, *Lycopodiopsis* Renault, 1890, and *Lycopodiophloios* Kräusel, 1961. Sommer and Trindade (1966) reviewed *Lycopodiopsis* and *Lycopodiophloios* and indicated that they are the only genera so far known from the Brazilian Gondwana, suggesting also that both genera were heterosporous. In his review of the lycopods, Chaloner (1967) placed all three southern hemisphere Permian genera in the Lycopodiopsidaceae. The defining characteristics of the family are: an absence of leaf cushions and, where fertile axes are known, sporophylls inserted directly on the main axis. Chaloner (1967) reproduced Seward's (1903) and Kräusel's (1961) illustrations; he also figured a specimen (1967, fig. 355) with closely spaced, diamond-shaped leaf scars which is clearly unlike all other specimens described as *Cyclodendron* and must be discounted as its affinities lie elsewhere.

Lycopodiopsis was described by Renault (1890) for permineralized vegetative axes. These axes, now called *Brasilodendron* Chaloner *et al.*, 1979, have typically closely spaced, diamond-shaped leaf scars and occasionally narrow leaves. These features alone contrast sufficiently with *Cyclodendron*,

but the new fertile material and axes with cuticle described here reinforce the separation of the two genera.

Kräusel (1961) erected the genus *Lycopodiophloios* for broad vegetative axes from Vereeniging. He interpreted some narrow leaves scattered in the matrix as having an organic connection to the axes. These axes have leaf scars identical to those of *Cyclodendron*. Kräusel regarded the striated surface of the axes and the diamond-shaped impressions flanking the leaf scars as sufficiently different from known *Cyclodendron* axes to require a new genus. In the absence of fertile axes of *Lycopodiophloios*, I think it unjustified to erect a new genus; I unite the sterile *Lycopodiophloios* axes with *Cyclodendron* on the basis of their epidermal features (identical size, shape, orientation of cells, and arrangement of stomata) and leaf scars (identical size, shape, arrangement in a low angled spiral, with ten to fourteen scars per gyre). I suggest that the diamond-shaped impressions associated with the scars and striations on broad axes (Kräusel's *Lycopodiophloios* and my Pl. 11, fig. 8), but absent on narrow axes, were features only of main stems which had reached a certain size. Kräusel reported no small, presumably juvenile, *Lycopodiophloios* axes whereas I have found all sizes of *Cyclodendron* from 8 mm to 8 cm. I believe that Kräusel's leafy specimen (1961, fig. 48) results from fortuitous accumulations of leaves close to the axis. Unfortunately, the two types of axis (i.e. the narrow *Cyclodendron* and the broad *Lycopodiophloios*) are unlikely to be found connected unless an almost complete specimen is discovered. I doubt also whether fertile *Lycopodiophloios* axes will ever be found since I interpret them as main stems which would not have carried sporangia. Rather than leave *Lycopodiophloios* as a permanent form genus, I unite these broad axes with *C. leslii*.

Cyclodendron contrasts with the two Carboniferous herbaceous genera from Argentina, *Bumbodendron* and *Malanzania* Archangelsky *et al.*, 1981. *Bumbodendron* is characterized by closely spaced fusiform leaf cushions, and *Malanzania* by false leaf scars and small spiny leaves. The resemblance of *Cyclodendron* to *Bothrodendron*, first noticed by Seward (1903), is superficial. *Bothrodendron* is a Carboniferous genus with small ligulate leaves and definite terminal cones, while *Cyclodendron* is apparently eligulate with large leaves and subterminal fertile zones. Similarly, *Caenodendron* Zalesky, 1918 from the lower Carboniferous has only superficially similar leaf scars.

The size of vegetative axes, up to 8 cm wide, suggests an arborescent habit for *C. leslii* (text-fig. 1A). Arborescent lycopods were uncommon after the Carboniferous, becoming extinct at the end of the lower Permian (Chaloner 1967). Kräusel (1961, figs. 32, 36–38) figured a single specimen which he considered fertile; he identified both megasporangia and microsporangia on the axis but I can see evidence only for megasporangia. This single fertile zone is on an impression fossil from Vereeniging (no *in situ* spores were recovered) and, since I have found several fertile axes which support either microsporangia or megasporangia but never both, I interpret *Cyclodendron* as having unisexual fertile zones. The presence of fertile zones rather than cones is a common feature in lower Carboniferous lycopods world-wide (Archangelsky *et al.* 1981). This type of organization persisted into the upper Carboniferous and, in the case of *Cyclodendron*, into the lower Permian of the Gondwana realm.

Du Toit (1932, p. 405) first stressed the importance of *C. leslii* as a potential index fossil, ranging from the 'Middle Ecca (Union) to the lowest Beaufort Beds (Wankie) and hence typically lower Permian'. *C. leslii* has also been reported from sediments of the same age in India (Maithy 1965). The extensive collections at the Bernard Price Institute support *C. leslii* as a lower Permian index fossil, with no evidence of the distinctive axes from younger sediments.

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